THERMAL EFFECTS ON FISH ECOLOGY

Of all environmental factors that influence aquatic organisms, temperature is the most all-pervasive. There is always an environmental temperature while other factors may or may not be present to exert their effects. Fish are, for all practical purposes, thermal conformers, or obligate poikilotherms. That is, they are able to exert little significant influence on maintaining a certain body temperature by specialized metabolic or behavioral means. Their body temperature thus fluctuates nearly in concert with the temperature of their aquatic medium (although particularly large, actively-moving fish such as tuna have deep muscle temperatures slightly higher than the water). Intimate contact at the gills of body fluids with the outside water and the high specific heat of water provide a very efficient heat exchanger that insures this near identity of internal and external temperatures.

Every response of fish, from incubation of the egg to feeding activity, digestive and metabolic processes, reproduction, geographic distribution, and even survival, proceeds within a thermal range dictated by the immediate environment. As human activities change this thermal environment, such as through deforestation, damming or thermal discharges from power stations, the activities of indigenous fish species must also change. Depending upon the magnitude and rates of the thermal changes, there may be minor readjustments of the rates of metabolism and growth, or major changes in the distribution of species and of the functioning of the affected aquatic ecosystems.

In our recent environmental awareness, we have coined the phrase "thermal pollution" for extensive thermal changes to natural aquatic environments that are believed to be detrimental to desired fish populations. The key to controlling "thermal pollution" is a firm understanding of how temperature affects fish, and of the circumstances that truly constitute pollution.

The subject of thermal effects on fishes has been given critical scientific review periodically over the past 25 years. (e.g. Fry, 1947; Bullock, 1955; Brett, 1956; Fry, 1964; Fry, 1967 and Brett, 1970). Scientific knowledge as a basis for controlling pollution is clearly more advanced in this area than than for almost any other environmental factor. This knowledge has been applied to the context of thermal modifications by electricity generating stations in two symposium volumes (Parker and Krenkel, 1969; Krenkel and Parker, 1969) and by Cairns (1968), Clark (1969), Parker and Krenkel (1969) and Coutant (1970 and 1972). The voluminous scientific literature on temperature effects on fishes may be easily searched for specific information in bibliographies by Kennedy and Mihursky (1967), Raney and Menzel (1969) and annual literature reviews by Coutant (1968, 1969, 1970, 1971) and Coutant and Goodyear (1972). Readers seeking more than a general review are advised to read these materials.

While fish must conform to water temperature, they have evolved mechanisms other than body temperature regulation to deal with vicissitudes of temperature fluctuations that occur geographically, seasonally and daily. That such mechanisms exist became apparent when fish physiologists realized that at any one temperature a fish may survive or die, be hyperactive or be numbed into activity, be stimulated to migrate or be passive, be sexually mature or remain immature, all depending upon the state of previous temperature exposures. Temperature affects organisms not only by absolute level (as in physics and chemistry) but also by change. Like light, temperature can exert effects through daily or seasonal patterns that exhibit a special quality beyond that of absolute level*.

The functional properties of temperature acting on fish can be summarized as follows: Temperature can act as a lethal agent that kills the fish directly, as a stressing agent that destroys the fish indirectly, as a controlling factor that sets the pace of metabolism and development, as a limiting factor that restricts activity and distribution, as a masking factor that interacts with other environmental factors by blocking or altering their potential expression, and as a directing agent in gradients

*Clear distinction must be made between *heat* which is a quantitative measure of energy of molecular motion that is dependant upon the mass of an object or body of water and *temperature* which is a measure (unrelated to mass) of energy intensity. Organisms respond to temperature, not to heat.

that stimulate sensory perception and orient activity. Each of these properties can be visualized as acting on two levels—on the individual fish and on the population of any one fish species.

Temperature as a Lethal Agent

Mass mortalities of fish in nature have often been reported, but usually the causes are obscure. Fish rarely die in places and at times when proper field instrumentation is operating or when trained observers are at hand. Many deaths probably go unnoticed, for scavengers may act quickly or water currents disperse carcasses (particularly of small fishes). The most common reports are of cold kills brought about by particularly severe winters or rapid drops in temperature (e.g. summaries by Brett, 1970). It is well known among fishery biologists that the abundance of a species reproduced in any one year varies tremendously, a fact that many scientists have attributed in part to deaths from unfavorable temperatures at early life stages when the fish are too small to be recognized as constituting a "fish kill".

Studies of temperature tolerance in fishes began in the last century. The early method of determining the lethal end-point (generally the cessation of opercular movements) by slow heating or cooling was generally supplanted in the 1940's by a more precise method of direct transfer to a series of preset temperatures in which the rates of dying of individual fish and the statistical variation among many individuals could be obtained. These experiments demonstrated the importance of recent past history of the fish, both the controlled holding temperature imposed in the laboratory prior to testing (acclimaton), and the seasonal environmental temperature when fish were tested directly from field collections (acclimatization).

These experiments also showed that each species of fish (and often each distinct life stage of one species) has a characteristic range of temperature that it will tolerate that is established by internal biochemical adjustments made while at the previous holding temperature (Figure 1). Ordinarily (for purposes of comparison) the upper and lower ends of this range are defined by survival of 50% of a sample of individuals similar in size, health and other factors, for a specified length of time, often one week. The tolerance range is shifted upward by long-term holding (acclimation) in warmer water, and downward by acclimation to cooler water. This accommodation is limited, however, at the lower end by freezing point of water (for species in

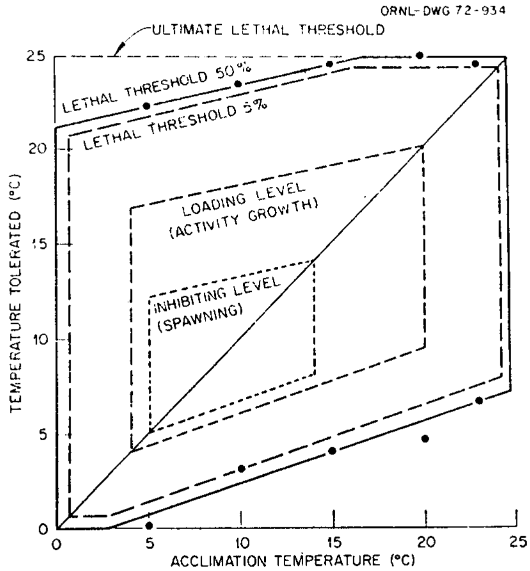

Figure 1 Upper and lower lethal temperatures for young sockeye salmon with various acclimation temperatures, plotted to show the ranges of tolerance, and within these ranges more restrictive requirements for activity, growth or spawning. (Reproduced by permission from Coutant, 1972.)

temperate latitudes) and at the upper end by an ultimate lethal threshold. The graphic representation (Figure 1) is a geometric figure for which an area can be computed. The areas (as degrees squared) provide conveneient measures of the relative overall sensitivity of tolerance among different species and life stages (a small area or zone on the graph signified high thermal sensitivity).

It is not surprising that rough species such as carp and goldfish were found to have large thermal tolerance zones.

Outside the thermal tolerance zone, premature death is inevitable and its onset is a function of both temperature and time of exposure (thermal resistance). Death occurs more rapidly the farther the temperature is from the threshold (Figure 2), an attribute common to the action of toxicants, pharmaceuticals, and radiation. The duration of survival of half of a test population of fish at extreme temperatures can be expressed as an equation based on experimental data for each acclimation temperature:

$$\log \text{survival time}_{(\text{min})} = a + b\,(\text{Temp}_{(^\circ\text{C})}),$$

in which a and b are intercept and slope of the linear regression lines in Figure 2. In some cases the time–temperature relationship is more complex than this semilogarithmic model, but this expression is the most generally applicable and is the one most generally accepted by the scientific

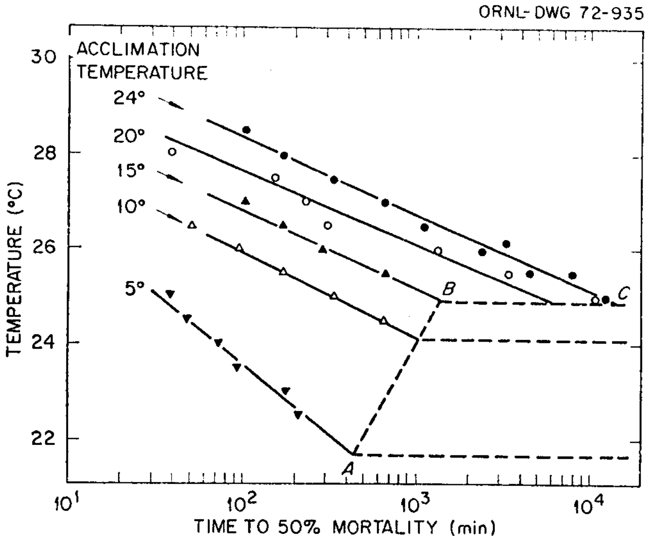

Figure 2 Median resistance times to high temperatures among young chinook salmon acclimated to the temperatures indicated. Line A–B denotes rising lethal threshold levels with increasing acclimation temperature. This rise ceases at higher acclimation temperatures. (Reproduced by permission from Coutant, 1972.)

community. The equation defines the average rate of dying at any extreme temperature.

The thermal resistance equations allow prediction of fish survival (or death) in zones where human activity induces extreme high temperatures. For example, juvenile salmon and trout were found to pass through warm mixing zones of thermal discharges to the Columbia River during their seaward migration (Becker *et al.*, 1971). The thermal exposure was a complex pattern of rapid temperature rise (often to temperatures beyond the tolerance zone) followed by a slow decline as the heated effluent mixed with the cooler river. By using the equation-expressed rates of dying at each of the temperatures briefly experienced, and the length of time the fish were exposed to each incremental temperature, the ability of the fish to survive the exposure was estimated and compared with actual field exposures. Similar predictions can be made for proposed thermal discharges, and corrective engineering can be selected before the project is constructed. Similar predictions can be made for circumstances where fish may become acclimated to warm water (e.g. in a discharge canal) and then be cooled rapidly and face a potential cold kill. This predictive methodology is further described by Coutant (1972).

Temperature as a Stressing Factor

Death need not come to fish directly from temperature or its change. In natural ecological systems death often comes as the result of a secondary agent acting upon a fish weakened by some stress such as temperature. This secondary agent is often disease or predator. A potentially lethal high temperature will, for example, induce loss of equilibrium before the physiological death point is reached, and equilibrium loss (going "belly-up") in a natural environment is an open invitation to predators. In fact, ongoing research indicates that stress from relatively small temperature changes (both up and down) will induce selective predation on the stressed fish. The effect appears to follow a time-temperature pattern similar to that for death, with stress appearing after shorter exposures and lower temperatures than required for death directly. The predictability developed for lethal responses can be applied to these stressing conditions as well, if we wish to prevent "ecological death."

Temperature as a Controlling Factor

a) Metabolism

Within the zone of thermal tolerance of any species (Figure 1), the most important contributor to survival and success in nature is the dynamic cycle of energy intake, conversion and utilization for activity, development (the differentiation of cells) and growth (multiplicaton of cells and storage of energy reserves). Since the time that Fry (1947) observed that environmental temperature controls energy metabolism, there has been extensive research in this area of fish physiology and biochemistry. This research has yielded important generalizations about the temperature responses of fish, and the physiological and biochemical "reasons" for these responses.

Metabolic processes are basically chemical in character. Among the most significant vital chemical reactions are the actions of the living catalysts (enzymes) which control the oxidation of organic food materials. Most enzymes show an optimum temperature at which they reach a maximum rate of catalytic activity. This is sometimes higher than the upper lethal threshold for the whole fish. The aggregate of many metabolic reactions also exhibits a temperature optimum, or point of maximum rate, which is often remarkably similar for various functions involved, for example digestion, development and locomotion (Figure 3). Through genetic selection, the optimum has become different for any two species. Below the optimum, the maximum rate possible is controlled by water temperature. These rates can be quite different for various functions. It should be noted that the optimum temperature and the maximum metabolic rates at any given temperature may be quite different during embryonic development and during the lifetime of the fully-developed fish.

Of the various methods that have been used to measure metabolic rates (see Brett, 1971), the most often measured has been the rate of oxygen consumption. This provides an instantaneous measure of enzyme activity so long as no oxygen debt, or delayed oxidation of certain chemical compounds, is accumulated. Three levels of metabolic rates have been commonly recognized for fish: (1) *Standard metabolic rate*, representing that fraction which is just necessary to maintain vital functions of a resting fish, (2) *routine metabolic rate* which also includes the energy demands of routine, spontaneous activity, and (3) *active metabolic rate* which represents the maximum level of oxygen consumed by a working (swimming) fish. The amount of energy available for active work (or growth) is termed the *metabolic scope* for activity, and it is the difference between active and standard metabolic rates. Each of these is related to temperature in a different way. The most important measure for a fish's ability to cope with the overall environmental demands in the metabolic scope, which has an optimum temperature (Figure 3).

b) Activity

As temperature controls the metabolic rate which provides energy for activity, that activity, then, is also controlled. The literature contains many references to increases in fish activity with temperature rise, particularly swimming performance. This increase in activity ceases at an optimum temperature that appears to coincide with the temperature of maximum metabolic scope (Figure 3).

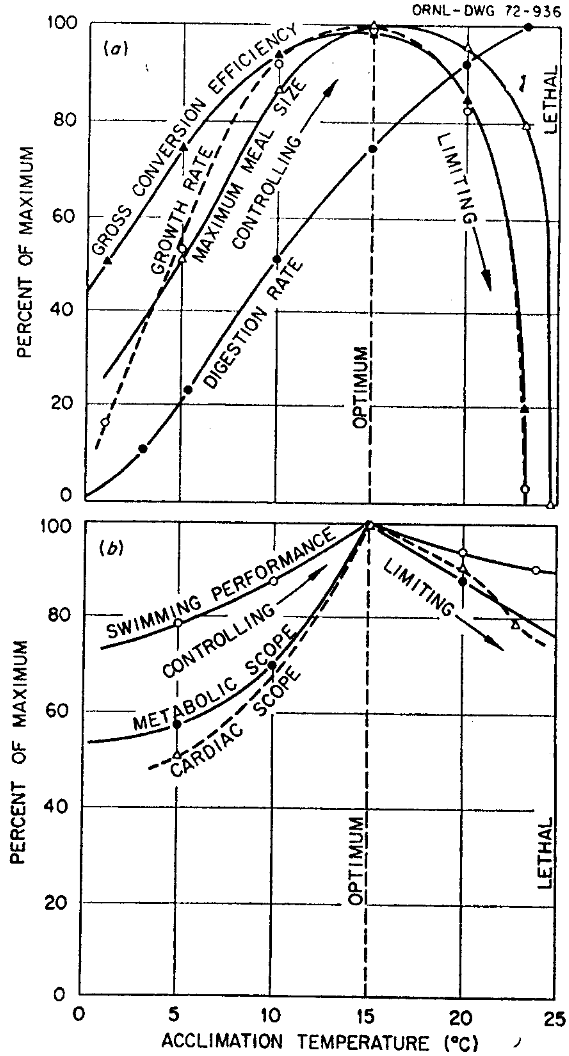

Figure 3 Performance of sockeye salmon in relation to acclimation temperature. There are three characteristic type responses, two have coinciding optima. (Reproduced by permission from Coutant, 1972.)

c) Growth

Temperature is one of the principal environmental factors controlling growth of fishes, others being light and salinity. There recently has been a considerable amount of laboratory experimentation to separate these often-correlated influences on growth.

Whenever there is abundant food, increasing temperature enhances growth rate up to an optimum (Figure 3) above which there is a decline. Low temperatures generally retard growth, although organisms residing habitually in cold areas such as the arctic have evolved metabolic compensations that allow good growth even at low extremes. Optimum growth appears to occur at about the same temperature as maximum metabolic scope. Restriction of food generally forces the optimum growth temperature toward cooler levels and restricts the maximum amount of growth attainable (Brett *et al.*, 1969).

Temperature as a Limiting Factor

As the previous discussion implied, there comes a point (the optimum) on a rising temperature scale at which increased temperature no longer speeds processes but begins to limit them. In contrast to the gradual increase in performance with temperature rise exhibited at sub-optimum temperatures, the responses at levels above optimum often show a precipitous decline (Figure 3). Performance is often reduced to zero several degrees below temperatures which would be directly lethal in the relatively short period of one week. One of the most significant of thermal limitations from the standpoint of a fish's overall success in his environment is upon net growth rate for the population. If a majority of individuals of the species cannot sustain positive growth, then the population is likely to succumb. While it is probably unnecessary for populations to grow at maximum rates, there must be a thermal maximum for prolonged exposures of any fish species that is less that the established lethal levels at which growth limitation becomes critical for continued population survival. The requirement for sustained growth may be one of the most important mechanisms of geographic limitations of species. Intensive research in this area is needed to establish rational upper temperature standards for water bodies.

Temperature as a Masking Factor

All other environmental factors, such as light, current, or chemical toxins, act upon fish simultaneously with a temperature regime. With so much of a fish's metabolic activity dependent upon temperature, both immediate and previous, it is little wonder that responses to other environmental factors change with differing temperature. The interactions are seemingly infinite, and the general impression that one obtains is that temperature is masking a clear-cut definition of the response pattern to any other environmental parameter.

This pessimism overstates the case, however. Two-factor experimentation is routine today, and interactions of temperature and a variety of pollutants are now becoming clear. For instance, research in Britain has shown that the effect of increased temperature on the toxicity of poisons to fish is generally to reduce their time of survival in relatively high lethal concentrations, but median *threshold* concentrations for death may not be markedly changed, or may even be increased (Ministry of Technology, 1968). An increase in temperature of 8 °C reduced the 48 hr LC_{50} (median lethal concentration) to rainbow trout by a factor of 1.8 for zinc (i.e. increased toxicity) but increased it (i.e. reduced toxicity) by about 1.2 for phenol, by 2.0 for undissociated ammonia, and by 2.5 for cyanide. The effect of temperature on ammonia toxicity is further expressed by changing the dissociation of ammonia in water and thus the percentage of actively toxic ammonia available. For estuarine and marine fishes temperature–salinity interactions are of special importance, and are receiving increased research attention.

Temperature as a Directing Agent

a) Gradient responses

Numerous observations of fish in horizontal and vertical thermal gradients both in the laboratory and under field conditions have demonstrated preferred or selected temperatures. There are wide differences among species, and some differences among life stages of any one species. The preferred temperature is dependent upon recent prior thermal history, but continuous exposure to a gradient (in which metabolic acclimation gradually takes place) results in a "final preferendum". Preferred ranges have been shown to coincide with the species-specific optimum temperature for maximum metabolic scope for activity, and thus the directive mechanism would appear to have survival value.

Many fish have a delicate sense for temperature discrimination. The threshold for teleosts (bony fish) appears to be on the order of ± 0.05°C, although elasmobranchs (sharks, rays) have a threshold quite a bit higher (about ± 0.8 °C). Orientation responses have generally been elicted by differences of about 0.5°C (Brett, 1971). Many fish are very capable of detecting undesirable temperatures and of avoiding water masses that are potentially detrimental to them.

b) Directive cues

A mechanistic response to temperature gradients is often overridden by seasonal influences and special behavior patterns involving temperature-orientated activities such as migration. The seasonal response to a specific temperature has been shown to have great importance for reproductive activity of a large number of fishes.

The sequence of events relating to gonad maturation, spawning migration, courting behavior, release of gametes, and subsequent development of egg and embryo represents one of the most complex phenomena in nature. While temperature cues appear critical in many cases, the interactions with other factors such as seasonal light intensity are still not clearly understood. Advance or retardation of reproduction has been closely related to temperature of the months preceeding spawning in such fish as the cod *Gadus morhua*. The difference in the effect of temperature governing a rate phenomenon (controlling or limiting) and temperature acting as or releasing factor is clearly shown in cases where falling temperatures induce spawning, as in the Pacific salmon.

Temperature appears to confine spawning to a narrower range than most other functions. The average range for spawning of marine fish is one-quarter to one-third that for the lethal range (Brett, 1971).

Summary

From this brief introduction, we can see that temperature is probably the preeminent master factor in the lives of fish. No study of fish in relation to their environment ("fish ecology") would be meaningful without consideration of thermal relationships. This review can direct the curious to more comprehensive treatises. From a different perspective, there are few environmental modifications that man could make to aquatic systems that would be so assured of causing some ecological change as temperature. Within limits, fish possess effective mechanisms for adapting to thermal changes, for such changes are a normal part of their existance. Man must be careful not to exceed these limits, however, if he wishes to preserve a productive commercial and recreational fishery.

REFERENCES

Becker, C. D., C. C. Coutant and E. F. Prentice, 1971. Experimental drifts of juvenile salmonids through effluent discharges at Hanford. Part II. 1969 Drifts and Conclusions. USAEC Rept. BNWL-1529, Battelle Northwest, Richland, Washington.

Brett, J. R., 1956. Some principles in the thermal requirements of fishes. *Quarterly Review of Biology* **31**(2): 75–87.

Brett, J. R., 1970. Temperature—Animals—Fishes. O. Kinne, Ed., in *Marine Ecology*, Vol. 1. Environmental Factors, Part 1. pp. 515–560.

Brett, J. R., 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *American Zoologist* **11**: 99–113.

Brett, J. R., J. E. Shelbourn and C. T. Shoop, 1969. Growth rate and body composition of fiingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *J. Fish. Res. Bd. Canada* **26**: 2363–2394.

Bullock, T. H., 1955. Compensation for temperature in the metabolism and activity of poikilotherms. *Biol. Rev.* **30**(3): 311–342.

Cairns, John, Jr., 1968. We're in hot water. *Scientist and Citizen* **10**(8): 187–198.

Clark, J. R., 1969. Thermal pollution and aquatic life. *Sci. Amer.* **220**(3): 18–27.

Coutant, C. C., 1968. Thermal pollution—Biological effects a review of the literature of 1967. *J. Water Poll. Cont. Fed.* **40**(6): 1047–1052.

Coutant, C. C., 1969. Thermal pollution—Biological effects a review of the literature of 1968. Battelle-Northwest, Richland, Wash.; BNWL-SA-2376, *J. Water Poll.* Cont. Fed. **41**(6): 1036–1053.

Coutant, C. C., 1970. Thermal Pollution—Biological effects a review of the literature of 1969. Battelle-Northwest, Richland, Wash.; BNWL-SA-3255, *J. Water Poll. Cont. Fed.* **42**(6): 1025–1057.

Coutant, C. C., 1970. Biological aspects of thermal pollution. I. Entrainment and discharge land effects. CRC Critical Reviews in *Environmental Control* **1**(3): 341–381.

Coutant, C. C., 1971. Thermal pollution—Biological effects. In: A review of literature of 1970 on wastewater and water pollution control. *J. Water Poll. Cont. Fed.* 43(6): 1292–1334.

Coutant, C. C., 1972. Biological Aspects of Thermal Pollution. II. Scientific basis for water temperature standards at power plants. CRC Crit. Rev. in *Envir. Control* (in press).

Coutant, C. C. and C. P. Goodyear 1972. Thermal effects. In A Review of the literature of 1971 on wastewater and water pollution control. *J. Water. Poll. Cont. Fed.* **44**(6): 1250–1294.

Fry, F. E. J., 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser. No. 55. Publ. Ont. Fish. Res. Lab. No. 68: 1–62.

Fry, F. E. J., 1964. Animals in aquatic environments: Fishes (Chap. 44). Handbood of Physiology, Section 4: Adaption to the Environment. Amer. Physiol Soc., Wash. D. C.

Fry, F. E. J., 1967. Responses of vertebrate poikilotherms to temperature. In *Thermobiology*, A. H. Rose (ed.) Academic Press, London. pp. 375–409.

Kennedy, V. S. and J. A. Mihursky, 1967. Bibliography on the effects of temperature in the aquatic environment. Univ. of Maryland, Nat. Res. Inst. Cont. No. 326. 89 p.

Krenkel, P. A. and F. L. Parker, 1969. *Biological Aspects of Thermal Pollution*, Vanderbilt Univ. Press, Nashville, Tennessee.

Ministry of Technology, U. K., 1968. Water pollution research 1967. p. 63.

Parker, F. L. and P. A. Krenkel, 1969b. Thermal pollution: Status of the art. Dept. of Envir. and Water Res. Eng., Vanderbilt Univ. Rept. No. 3.

Parker, F. L. and P. A. Krenkel, 1969a. *Engineering Aspects of Thermal Pollution*. Vanderbilt Univ. Press, Nashville, Tennessee.

Raney, E. C. and B. W. Menzel, 1969. Heated effluents and effects on aquatic life with emphasis on fishes: A bibliography. Ichthyological Associates Bull. No. 2 prepared with Cornell Univ. Water Resources and Marine Sciences Center and Philadelphia Electric Company. 470 p.

CHARLES C. COUTANT
Oak Ridge National Laboratory